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Taxonomy of the genus *Lycalopex* (Carnivora: Canidae) in Argentina

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Abstract.—Previously treated as species of *Pseudalopex,* Argentine members of the genus *Lycalopex* (*L. griseus, L. gymnocercus,* and *L. culpaeus*) are examined to clarify the taxonomic status of each named form. Principal components analyses of 26 cranial measurements of 151 adult specimens and 11 pelage characters of 111 specimens, clearly distinguish *L. culpaeus* from the other two taxa. *Lycalopex griseus* and *L. gymnocercus* show clinal variation in cranial measurements and pelage characters. Qualitative cranial characters, traditionally used as diagnostic for *L. griseus* and *L. gymnocercus,* revealed great nongeographic variation. We conclude that *L. griseus* and *L. gymnocercus* are conspecific, and should be known as *L. gymnocercus.* Therefore, we recognize only two species of the genus *Lycalopex* (*L. culpaeus* and *L. gymnocercus*) in Argentina. We also use this opportunity to review synonymies of the recognized species in *Lycalopex.*

Although the taxonomic status of South American canids has been reviewed at length, classification at generic and subgeneric levels has not been completely resolved (Berta 1988, Kraglievich 1930, Langguth 1975). Three of the living Argentine foxes (*Lycalopex culpaeus, L. gymnocercus,* and *L. griseus*) have been alternatively included in the genera: *Pseudalopex* Burmeister, 1856 (Cabrera 1931, 1932, 1940; Thomas 1914a; Berta 1987, 1988; Nowak 1991; Wozencraft 1993), *Dusicyon* Hamilton-Smith, 1839 (Cabrera 1958, Corbet and Hill 1991, Clutton-Brock et al. 1976, Langguth 1969, Osgood 1934, Simpson 1945, Wozencraft 1989), or *Canis* Linnaeus, 1758 (Kraglievich 1930, Langguth 1975, Van Gelder 1978). Their inclusion in each of these genera was based on the degree of comparability with *D. australis* (Kerr, 1792), type species of genus *Dusicyon,* as determined from studies of external, cranial, and dental characters. Cabrera (1931, 1932) and Berta (1987, 1988) suggested that *culpaeus, gymnocercus,* and *griseus* were sufficiently different from *D. australis* to place them in the genus *Pseudalopex,* an arrangement followed by Wozencraft (1993). Cabrera (1931, 1958) considered *Lycalopex* Burmeister, 1854 (type species *Canis vetulus* Lund) separate from *Pseudalopex* Burmeister, 1856 (type species *Canis magellanicus* Gray). However, Berta (1987, 1988) and Wozencraft (1993) treated them as congeneric, but used *Pseudalopex* for the genus. Corbet and Hill (1991) also treated them as congeneric, but used *Dusicyon* for the genus. We follow Berta and Wozencraft in treating *Lycalopex vetulus* as congeneric with species previously assigned to *Pseudalopex,* but use *Lycalopex* as the valid generic name because it has two-years priority.

The taxonomic status of Argentine foxes has rarely been evaluated since their original descriptions. Three living species of genus *Lycalopex* currently are recognized in Argentina: the culpeo fox, *L. culpaeus,*

which inhabits mainly grasslands (pampas) and deciduous forests from southern Patagonia to Ecuador; the patagonian gray fox, *L. griseus,* which occurs from Atacama, Chile, and Santiago del Estero, Argentina, south to Tierra del Fuego, and is sympatric with *L. culpaeus* in part of its range; and the pampas gray fox, *L. gymnocercus,* which inhabits the humid grasslands (pampas) in southern Brazil, northern Argentina, Uruguay, Paraguay, and eastern Bolivia (Cabrera & Yepes 1940, Cabrera 1958, Nowak 1991, Wozencraft 1993). However, information on distributional limits of *L. griseus* and *L. gymnocercus* in central Argentina, especially in the provinces of La Pampa, Córdoba, and San Luis, is scanty (Kraglievich 1930, Cabrera 1932).

Clutton-Brock et al. (1976) concluded that *L. culpaeus* and *L. gymnocercus* were phenetically close, and suggested that they should be considered conspecific because of cranial and pelage similarities. The skull of *L. griseus* has little to distinguish it from that of *L. culpaeus* except for smaller size and lack of an interparietal crest.

Our objectives in this paper are to analyze geographic variations of dental, cranial, and pelage characters and to evaluate the taxonomic relationships of *L. culpaeus, L. gymnocercus,* and *L. griseus.* We also use this opportunity to correct several errors, omissions, and misallocations of names discovered during our research, and to provide a synonymy that includes first usage of unique name combinations applied to the recognized species in *Lycalopex.*

Materials and Methods

We examined 151 skulls and 111 skins (see Appendix 1) deposited in the following collections: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and Instituto Miguel Lillo de Tucumán (IML).

We used only specimens of adults with intact skulls and complete data in the statistical analyses. We considered specimens to be adult if the basisphenoid-basioccipital suture was closed and the permanent dentition was complete. We measured 30 cranial and dental characters with a dial caliper to the nearest 0.1 mm on each skull, with bilateral characters always measured on the left side.

Measurements are defined as follows: 1) condylobasal length: distance from anterior edge of premaxillae to posteriormost surface of occipital condyles; 2) palatal length: distance from anterior margin of premaxillae to anteriormost point on posterior edge of palate; 3) minimum rostral length: distance from anterior margin of premaxillae to anteriormost orbital margin; 4) facial length: distance from anterior edge of premaxillae to posterior end of nasal bones; 5) bullar length: from sharp anterior end of tympanic bulla diagonally to posterior margin adjacent to paroccipital process; 6) maxillary toothrow length: alveolar length of upper toothrow including canine and second upper molar; 7) P4–M2 length: alveolar length of upper toothrow including fourth upper premolar and second upper molar; 8) minimum rostral height: rostral height behind canines; 9) height of braincase: height measured at right angle to basisphenoid, excluding sagittal crest; 10) interorbital constriction: least distance between orbits; 11) postorbital constriction: least distance across constriction just posterior to postorbital processes; 12) rostral width at canines: width across the rostrum at canines, measured from outer margins of alveoli; 13) rostral width at first upper molars: width across the rostrum at first upper molars, measured from outer margins of alveoli; 14) zygomatic breadth: greatest distance across outer margins of zygomatic arches; 15) mastoidal width: greatest distance across mastoid processes; 16) braincase width; greatest width across parietals; 17) width across occipital condyles: greatest distance between outer margins of occipital condyles; 18) width between postglenoid processes: least distance between inner margins of postglenoid processes; 19) P4

length: greatest alveolar length of fourth upper premolar; 20) P4 width: greatest alveolar width of fourth upper premolar; 21) ml length: greatest alveolar length of first lower molar; 22) ml width: greatest alveolar width of first lower molar; 23) rostral height at P2-P3: rostral height measured between second and third upper premolars; 24) mandibular length: length of mandible from anteriormost part of mandibular symphysis to posteriormost part of articular process; 25) mandibular toothrow length: alveolar length of lower toothrow including canine and third lower molar; 26) m1–m3 length: alveolar length of lower molars; 27) alveolar length of upper canine: greatest alveolar length of upper canine; 28) nares length: distance from anterior margin of premaxillae to anteriormost margin of nasal bones; 29) width across postorbital processes: greatest distance across outer margins of postorbital processes; 30) length between postorbital constriction and postorbital processes: least distance measured along sagittal suture. The last four measurements were not included in statistical analyses due to their high individual variability.

We grouped collecting sites of gray foxes into six OTUs, each representing a geographically discrete region (Fig. 1, Appendix 1). One specimen from La Paz, Mendoza, coded as unknown, was assigned to the central-western (CWT) OTU using a stepwise discriminant-function analysis with a probability of 61%. All specimens of *L. culpaeus* were included in a single OTU.

Sexual dimorphism was assessed only in the gray fox CCT OTU (19 ♂♂, 14 ♀♀) by multivariate analysis of variance (MANOVA) and discriminant-function analysis. Samples for the other taxa were too small to evaluate for dimorphism.

The mean and standard deviation of each measurement were calculated for each OTU. Principal component analysis was done using NT-SYS programs (Rohlf 1992) to assess phenetic overlap among individuals. Each character was standardized to a mean of zero and a standard deviation of one.

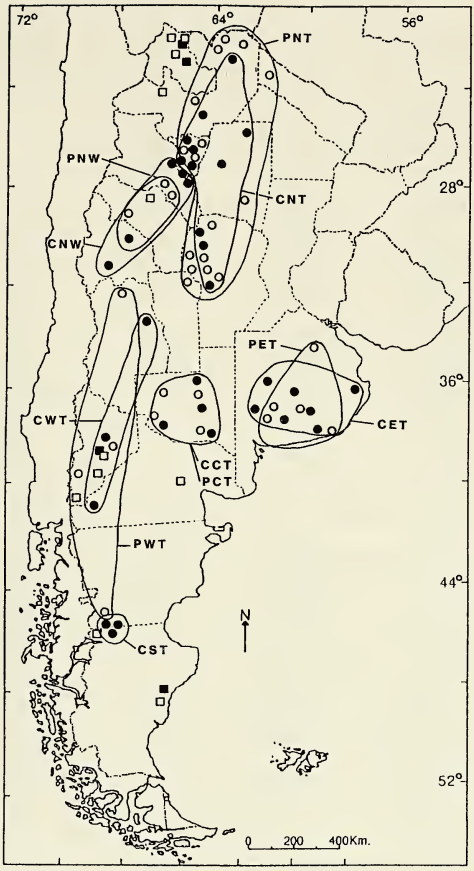

Fig. 1. Map of Argentina showing collecting sites for specimens listed in Appendix 1. Squares indicate culpeo foxes; circles or dots, gray foxes; solid symbols correspond to specimens used in cranial analyses; open symbols indicate specimens used in pelage analysis. Abbreviations refer to OTUs, which are identified in Appendix 1.

Environmental factors vary greatly over the ranges of latitude (approximately 24°) and elevation (sea level to over 3000 meters) represented by the samples analyzed. Therefore, to determine if variation in size was associated with environmental factors, a second principal component analysis was performed using the means of measurements for each OTU. Pearson's correlation coefficients were calculated between the first principal component scores and lati-

tude, longitude, elevation, mean annual temperature, and average annual rainfall. Since each OTU comprised more than one collecting site, weighted means were calculated for each environmental factor.

Kraglievich (1930) used two cranial characters (crests on the skull and distance between postorbital constriction and postorbital processes) to distinguish *gymnocercus* from *patagonicus* (= *griseus* of authors). He believed that the presence of a sagittal crest and a long interorbital region distinguished *gymnocercus* from *patagonicus,* which he identified as having a lyriform sagittal area and a short distance between postorbital constriction and postorbital processes. We examined geographic and nongeographic variation of both characters in a sample of 81 specimens representing areas from which only the presence of *gymnocercus* had been cited. We scored three possible conditions for each character as follows: Temporal ridges, A) fused to form a well-developed sagittal crest, B) not fused and enclosing a narrow lyriform sagittal area, or C) not fused and enclosing a wide lyriform sagittal area; distance between postorbital constriction and postorbital processes: A) long (10.0–15.0 mm), B) medium (7.0–9.0 mm) or C) short (4.0–6.0 mm).

We analyzed geographic variation in 11 pelage characters (as described by Cabrera 1932) with color determinations made under natural light. Characters were scored as follows: A) chin spot: absent = 0, poorly marked = 1, very dark = 2; B) thigh spot: absent = 0, poorly marked = 1, very dark = 2; C) dorsal longitudinal band: absent = 0, poorly marked = 1, very dark = 2; D) underparts: brownish = 0, cream = 1, gray = 2; E) sides: reddish = 0, brownish = 1, gray = 2; F) upperparts: reddish = 0, gray = 1, brownish = 2; G) dorsal guard hairs banded (agouti): fine = 0, intermediate = 1, thick = 2; H) length of dorsal guard = hairs: short = 0, medium = 1, long = 1; I) ears: reddish = 0, pale brown = 1, dark brown = 2; J) head: reddish = 0, gray = 1, brownish = 2; K) thigh: reddish = 0, brownish = 1, gray = 2. Specimens were grouped into six OTUs, each representing a geographically discrete region (Fig. 1, Appendix 1). We used principal component analysis to evaluate phenetic overlap.

We also examined the microscopic structure of dorsal guard hairs taken from 48 specimens including both gray and culpeo foxes. Samples were first washed in an alcohol-ether solution (1:1) and then bleached for 24 hours in hydrogen peroxide. Then hairs were washed with fresh water, fixed to a glass slide with a thin layer of vinilic glue, and examined at 320 diameters. Type and disposition of cuticular scales and the type of medulla follow the nomenclature adopted by Chehébar & Martín (1989).

Results

Cranial characters.—Multivariate analysis of variance (MANOVA) of the gray fox CCT OTU revealed no significant sexual dimorphism ($P = 0.62$; $n = 33$) in 20 of the 26 measurements analyzed. Discriminant analysis showed an overlap between sexes with females being more variable.

Skulls of *L. culpaeus* (CCU OTU) clearly are larger than those of the other groups, which are all gray foxes (see Table 1 for means and standard deviations). Braincase width (16) was one of the more important measurements for separating gray and culpeo foxes. The skulls of the gray fox OTUs are not only smaller, but show little variation except for size increase toward the east and northeast, suggesting that variation is clinal.

All variables in the principal components analysis had positive correlations on component I, which indicates a general size factor (Table 2). The second component was bipolar, with both positive and negative loadings. The first component (Fig. 2) clearly separated *L. culpaeus* (CCU) from the gray foxes (*griseus* and *gymnocercus*). The OTUs of gray foxes overlapped with a general increase in size from west to east.

Table 1.—Cranial measurements for Argentine culpeo and gray foxes. Mean and one standard deviation (in parentheses) for each sample (OTU; sample acronym over sample size) measured. Measurements (left column) defined in text; OTUs identified in Appendix 1 under specimens examined for cranial analysis.

	CCU 58	CST 7	CWT 14	CNW 8	CCT 33	CET 15	CNT 16
1	164.66	122.69	122.83	122.98	138.79	141.53	125.91
	(7.13)	(4.15)	(4.12)	(8.90)	(5.44)	(7.56)	(2.86)
2	85.87	64.80	65.11	64.49	71.95	72.79	64.90
	(3.92)	(3.36)	(2.29)	(5.70)	(2.92)	(3.56)	(2.22)
3	73.59	54.09	53.74	52.39	60.49	61.24	53.81
	(4.50)	(3.04)	(2.45)	(4.93)	(3.19)	(3.77)	(2.32)
4	81.36	60.00	59.91	57.03	68.21	68.81	59.01
	(4.65)	(3.72)	(3.43)	(6.52)	(2.72)	(4.77)	(2.90)
5	20.66	18.44	17.90	18.39	18.92	19.76	19.91
	(1.02)	(1.07)	(1.19)	(0.73)	(1.25)	(0.93)	(0.97)
6	20.99	15.19	14.83	15.64	17.60	17.97	16.24
	(1.53)	(0.92)	(1.05)	(1.44)	(1.25)	(1.18)	(1.13)
7	43.66	38.19	38.19	37.88	40.15	40.10	38.03
	(1.20)	(0.76)	(1.21)	(2.75)	(1.15)	(1.57)	(1.80)
8	24.99	20.00	18.84	19.16	21.79	22.66	20.44
	(1.67)	(1.03)	(1.37)	(1.86)	(1.35)	(1.66)	(0.75)
9	73.66	58.66	58.32	57.06	63.01	63.50	57.93
	(2.81)	(1.66)	(1.72)	(4.09)	(2.42)	(2.91)	(1.91)
10	30.42	25.71	25.34	25.76	27.41	27.85	26.40
	(1.29)	(0.86)	(1.22)	(1.69)	(1.12)	(1.22)	(1.05)
11	16.52	12.97	12.84	12.79	13.79	14.19	13.19
	(0.87)	(0.42)	(0.71)	(0.91)	(0.77)	(0.57)	(0.66)
12	7.86	6.06	5.98	6.46	6.92	7.00	6.66
	(0.49)	(0.28)	(0.51)	(0.49)	(0.44)	(0.35)	(0.37)
13	16.77	13.73	13.62	13.40	14.88	15.11	14.00
	(0.83)	(0.40)	(0.89)	(1.31)	(0.71)	(0.98)	(0.73)
14	7.01	5.67	5.70	5.78	6.20	6.25	5.84
	(0.37)	(0.20)	(0.36)	(0.42)	(0.32)	(0.42)	(0.31)
15	128.61	95.40	94.35	93.61	106.57	108.78	96.79
	(6.10)	(4.27)	(3.51)	(8.38)	(4.40)	(5.85)	(2.59)
16	83.51	65.14	64.94	63.81	70.55	71.01	65.44
	(3.30)	(2.05)	(2.29)	(5.02)	(2.81)	(3.33)	(1.93)
17	29.58	24.71	24.58	25.03	26.53	27.06	25.50
	(1.12)	(0.98)	(1.14)	(1.66)	(1.28)	(1.10)	(0.91)
18	28.15	23.04	21.94	21.48	25.51	26.47	23.19
	(1.94)	(1.41)	(1.45)	(2.50)	(1.55)	(2.30)	(1.61)
19	26.55	25.33	24.19	23.65	25.18	25.53	24.19
	(1.86)	(1.28)	(1.35)	(1.25)	(1.68)	(1.67)	(1.65)
20	27.51	19.21	18.67	19.75	22.50	23.20	20.59
	(1.84)	(1.11)	(0.91)	(2.05)	(1.26)	(1.73)	(0.97)
21	46.70	36.74	35.07	37.25	40.39	42.00	38.72
	(1.80)	(1.51)	(1.76)	(2.45)	(1.95)	(2.09)	(0.97)
22	88.79	64.27	63.27	65.06	73.59	75.53	67.60
	(5.32)	(2.52)	(2.09)	(5.71)	(3.54)	(4.46)	(2.09)
23	54.75	42.49	41.95	42.00	46.62	48.13	44.53
	(2.50)	(1.43)	(1.10)	(2.89)	(1.88)	(2.99)	(1.23)
24	51.88	44.66	44.30	44.05	46.76	46.93	44.58
	(1.48)	(0.94)	(0.86)	(1.65)	(1.42)	(1.97)	(0.91)
25	29.79	23.34	23.59	23.95	26.02	25.93	24.35
	(1.63)	(1.18)	(1.41)	(2.08)	(1.48)	(1.39)	(0.92)
26	38.48	31.47	31.22	31.85	34.32	34.53	33.13
	(1.39)	(0.96)	(0.80)	(1.47)	(1.59)	(1.78)	(1.21)

Table 2.—Character loadings of cranial variables of Argentine culpeo and gray foxes (n = 151) on the first two principal components. Measurements defined in text.

Variable	Component I	Component II	Variable	Component I	Component II
1	0.211	−0.037	14	0.193	−0.103
2	0.209	−0.042	15	0.210	−0.026
3	0.205	−0.041	16	0.208	−0.059
4	0.206	0.021	17	0.197	−0.143
5	0.149	0.022	18	0.184	0.286
6	0.197	0.012	19	0.108	0.885
7	0.191	0.111	20	0.206	0.029
8	0.192	−0.228	21	0.205	−0.012
9	0.208	−0.060	22	0.206	0.064
10	0.198	−0.132	23	0.206	0.003
11	0.199	−0.107	24	0.203	0.078
12	0.184	−0.250	25	0.197	−0.096
13	0.194	−0.109	26	0.200	0.024
			% variance	84.68	3.26

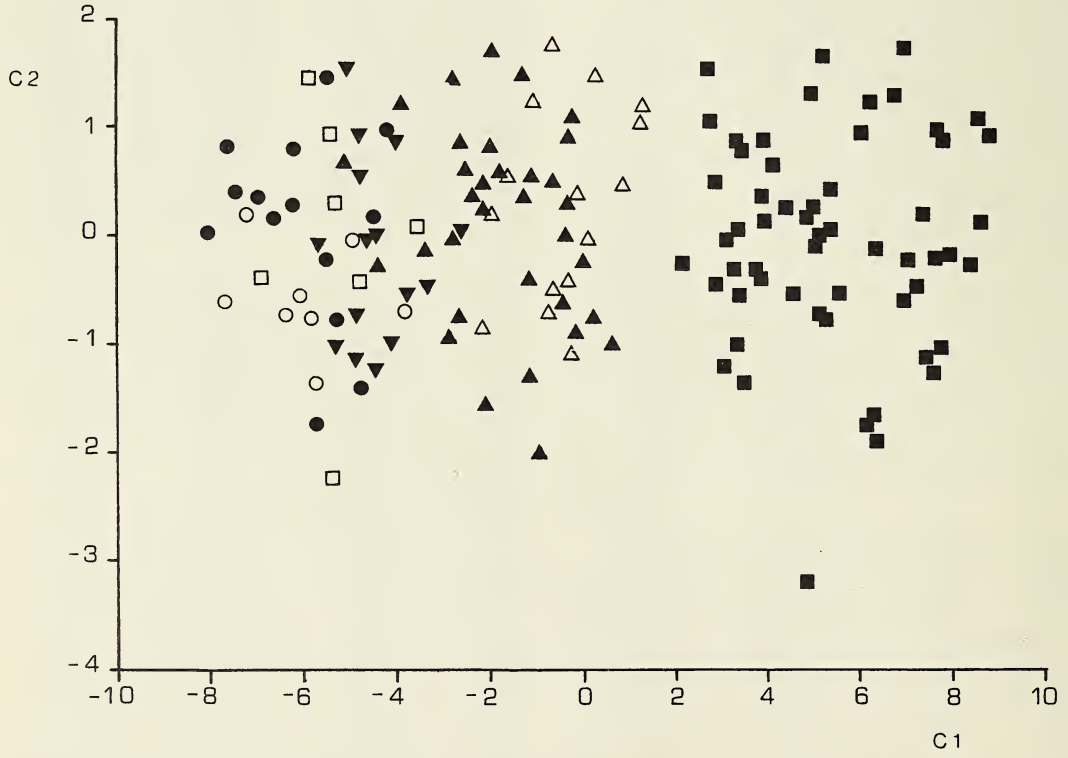

Fig. 2. Distribution of 151 specimens of Argentine foxes based on cranial data on the first two principal components. Symbols represent OTUs, identified in Appendix 1 under cranial analysis, as follows: ■—CCU; □—CST; ●—CWT; ○—CNW; ▲—CCT; △—CET; ▼—CNT.

Table 3.—Argentine gray foxes from areas where only *gymnocercus* was believed to occur, segregated on the basis of three developmental conditions of temporal ridges and three comparative lengths of interorbital region of the skull. Development of temporal ridges: A, fused into sagittal crest; B, not fused and enclosing narrow lyriform sagittal area; C, not fused and enclosing wide lyriform sagittal area. Distance in midline from plane of interorbital constriction to plane of postorbital processes: A, long (10.0–15.0 mm); B, medium (7.0–9.0 mm); C, short (4.0–6.0 mm).

Condition	Temporal ridges	Interorbital distance
A	15 (19%)	33 (41%)
B	23 (28%)	20 (25%)
C	43 (53%)	28 (34%)
Total	81	81

Table 4.—Character loadings of coded pelage variables of Argentine foxes (n = 111) on the first two principal components.

Variable	PC I	PC II
A	0.392	−0.010
B	0.355	−0.201
C	0.118	0.548
D	−0.173	0.108
E	0.318	−0.313
F	0.234	−0.281
G	0.195	0.326
H	0.217	0.551
I	0.354	0.068
J	0.372	0.159
K	0.414	−0.173
% of variance	43.00	14.81

The La Pampa OTU (CCT) was the most variable (Fig. 2), spanning the gap between the western OTUs and the Buenos Aires sample (CET).

In the analysis based on means of gray fox OTUs, the first component explained 90.9% of the variance. As all variables had a positive loading, component I represents a general size factor. First component scores showed a significant positive correlation with rainfall (r = 0.90; $P < 0.05$) which increases toward the northeast.

Cranial characters of Argentine gray foxes are highly variable. Our analysis (Table 3) of the development of temporal ridges and length of interorbital region, once considered diagnostic for separating *griseus* from *gymnocercus,* shows that these cranial features have little or no value for distinguishing among gray foxes.

Pelage characters.—Principal components analysis of pelage characters showed high variation among the groups (Table 4, Fig. 3) with the first two components explaining only 57.8% of the variance. However, these results are in agreement with the principal component analysis based on cranial characters; in both analyses the culpeo foxes (*culpaeus*) are clearly separated from the gray foxes (*griseus* and *gymnocercus*).

The *L. culpaeus* group differs from the other groups in the completely white chin and the reddish thigh lacking a posterior dark spot. Patterns of gray fox pelage characteristics can be correlated with geographic areas represented by the OTUs (Table 5).

Microscopic examination of guard hairs revealed no differences in either the type of medulla or the type and arrangement of cuticular scales. The medulla is segmented and scales are lanceolate and imbricated in all skins examined.

Discussion and Conclusions

We found no significant sexual dimorphism in gray foxes; small samples sizes precluded testing for sexual dimorphism in culpeo foxes. The absence of sexual dimorphism has been reported in other canids (Waithman & Roest 1977, Gingerich & Winkler 1979).

Multivariate analyses of both cranial and pelage characters confirm that *L. culpaeus* differs significantly from gray foxes in Argentina. These differences support species status for *L. culpaeus* and argue against the Clutton-Brock et al. (1976) conclusion that culpeo and gray foxes are phenetically close and might be conspecific.

Gray foxes, however, show clinal variation in skull size correlated with increasing annual precipitation. Gray foxes also are

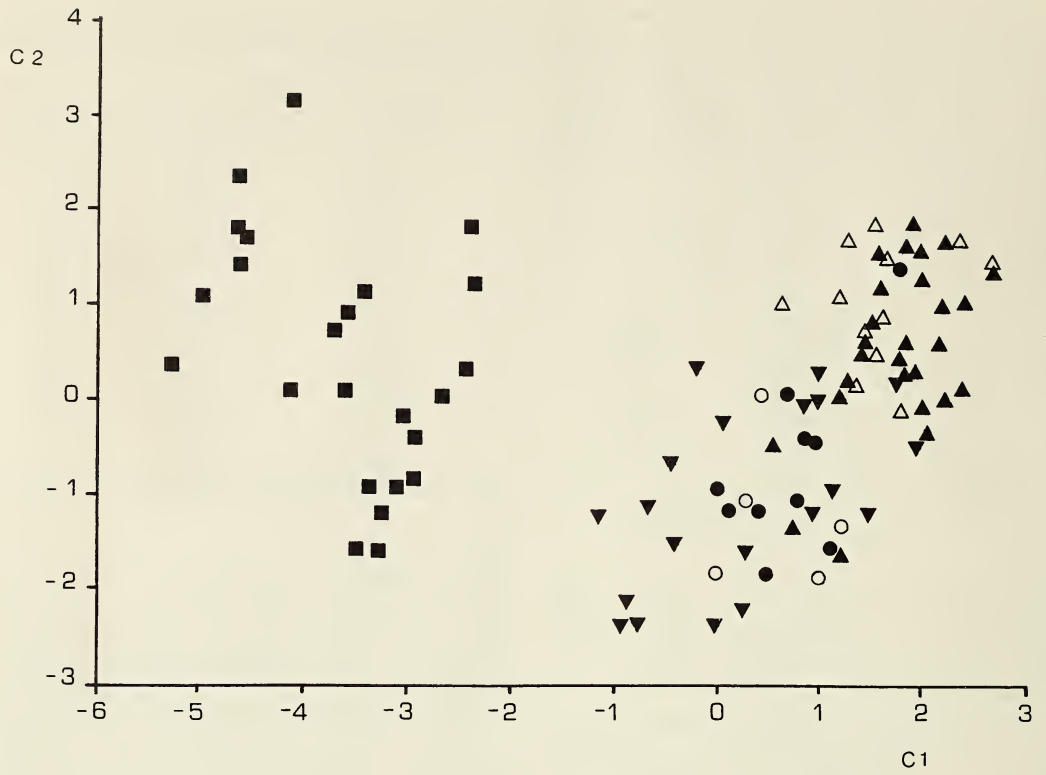

Fig. 3. Distribution of 111 specimens of Argentine foxes based on pelage characters on the first two principal components. Symbols represent OTUs, identified in Appendix 1 under pelage, as follows: ■—PCU; △—PET; ○—PNW; ▼—PNT; ●—PWT; ▲—PCT.

Table 5.—Qualitative pelage characteristics of Argentine gray foxes. Pelage characters described in text; OTUs identified in Appendix 1 under specimens examined for pelage analysis; OTU acronym followed by sample size in parentheses.

Character	PNW (6)	PWT (9)	PNT (25)	PET (14)	PCT (30)
Chin spot	Very dark	Variable-dark	Very dark	Very dark	Very dark
Thigh spot	Very dark	Variable-dark	Very dark	Very dark	Very dark
Dorsal band	Absent–poorly marked	Absent–poorly marked	Absent–poorly marked	Very dark	Variable
Underparts	Brownish	Cream	Brownish-cream	Cream	Brownish-cream
Sides	Brownish	Brownish-gray	Brownish-gray	Brownish	Brownish
Upperparts	Brownish	Brownish	Brownish	Brownish	Brownish
Agouti	Fine–medium	Fine–very fine	Fine–medium	Thick–medium	Variable
Guard hair length	Variable	Variable	Variable	Variable	Variable
Ears	Reddish	Dark brown	Reddish-pale brown	Pale brown	Variable-brown
Head	Reddish	Brownish	Reddish-brownish	Brownish	Brownish
Thigh	Reddish	Reddish	Brownish	Brownish	Brownish

smaller when sympatric with *L. culpaeus*. Data on geographic variation and clinal trends in size of canids are scarce. Fuentes & Jaksic (1979) found clinal variation in size from north to south in *L. culpaeus* and *L. griseus* in Chile, and suggested that progressive increments of habitat overlap towards the south were compensated by progressively greater differences in body size and in mean prey size.

We found the cranial characters used by Kraglievich (1930) to distinguish *L. gymnocercus* from *L. griseus* to be highly variable even within the same population. Kraglievich (1930:51) claimed that *gymnocercus* frequently has an extensive sagittal crest and a greater distance between the interorbital region and postorbital processes than has *patagonicus* (= *griseus* of authors). We scored three possible conditions for each of these two cranial characters in 81 gray foxes previously identified as *gymnocercus* from areas where only *gymnocercus* had been assumed to occur. Our results (Table 3) showed high individual and geographic variation indicating that the characters have little or no taxonomic value for discriminating among gray foxes. Kraglievich (1930) also considered postorbital constriction (measurement 11) to be narrower in *gymnocercus* than in *patagonicus* (= *griseus* of authors), but our analysis revealed relatively little variation when all groups of gray foxes are compared (Table 1).

Most of the morphological differences ascribed to the named forms of gray foxes had been based on type specimens, which for *griseus* and *gymnocercus* come from localities approximately 3500 km apart. Some of these characters, once considered diagnostic, have not proven useful for taxonomic purposes. For example, in accord with Clutton Brock et al. (1976), our results suggest that the absence of a sagittal crest in canids may be associated with small size.

Chromosomal analyses of these species (Gallardo & Formas 1975, Vitullo & Zuleta 1992) show a 2N = 74, NF = 76 karyotype with all-acrocentric autosomes. This karyotype, considered primitive for South American canids, does not distinguish among these species.

Because our samples of gray foxes showed clinal variation in size and color pattern as well as considerable nongeographic variation in qualitative characters considered diagnostic by previous workers, we conclude that gray foxes of Argentina are conspecific. *Lycalopex gymnocercus* is the oldest available name for the gray foxes of Argentina.

Taxonomy

Lycalopex Burmeister, 1854

Synonyms.—

Canis: Molina, 1782:293 (not *Canis* Linnaeus, 1758).

Vulpes: Martin, 1837:11 (not *Vulpes* Frisch, 1775).

Procyon: Fischer, 1814:178 (not *Procyon* Storr, 1780).

Dusicyon Hamilton-Smith, 1839:248 (part; described as a section of *Chaon* Hamilton-Smith, 1839).

Cerdocyon Hamilton-Smith, 1839:259 (part; described as a section of *Chaon* Hamilton-Smith, 1839).

Lycalopex Burmeister, 1854:95 (described as a section of *Canis* Linnaeus); type species *Canis vetulus* Lund, 1842a, by subsequent designation (Thomas 1914a: 352).

Pseudalopex Burmeister, 1856:24 (described as a section of *Canis* Linnaeus); type species *Canis magellanicus* Gray, 1837a (= *Vulpes magellanicus* Gray, 1837b), by subsequent designation (Thomas 1914a:352).

Thous: Gray, 1869:514 (part; not *Thous* Hamilton-Smith, 1839).

Lupulus: Trouessart, 1897:304 (part; not *Lupulus* Blainville, 1830).

Nothocyon: Wortman and Matthew, 1899: 124 (part; not *Nothocyon* Matthew, 1899).

Pseudolopex Philippi, 1903:157 (incorrect

subsequent spelling of *Pseudalopex* Burmeister, 1856).

Pseudolycos Philippi, 1903:157; proposed as a subgenus of "unsere grösseren Füchse" (our larger foxes [Chilean]); no species mentioned.

Eunothocyon J. A. Allen, 1905:152; type species *Canis sladeni* Thomas, 1904, by original designation.

Angusticeps Hilzheimer, 1906:114 (proposed as a subgenus of *Canis* Linnaeus, 1758); type species *Canis* (*Angusticeps*) *reissi* Hilzheimer, 1906, by monotypy.

Viverriceps Hilzheimer, 1906:116 (*lapsus* for *Angusticeps*; not *Viverriceps* Gray, 1867).

Microcyon Trouessart, 1906:1186 (proposed as a subgenus of *Speothos* Lund, 1839a); type species *Speothos riveti* Trouessart, 1906, by original designation.

Lycalopex culpaeus (Molina, 1782)

Synonyms.—

Canis culpaeus Molina, 1782:293; type locality "Chili," restricted to "Santiago province" by Cabrera (1931:62).

C[*anis*]. *Vulpes chilensis* Kerr, 1792:144; type locality "Chili." Based exclusively on *Canis culpaeus* Molina.

C[*anis*]. *Magellanicus* Gray, 1837a:88 (*nomen nudum*).

Vúlpes magellánica Gray, 1837b:578; type locality "Magellan's Straits" [= Port Famine; Gray 1843:61], Magellanes, Chile.

Cerdocyon Magellanicus: Hamilton-Smith, 1839:266 (name combination).

Canis (*Pseudalopex*) *lycoides* Philippi, 1896:542 (p. 2 in reprint); type locality "insulis Tierra del Fuego" [= Bahía Felipe; Wolffsohn 1921:514], Magellanes, Chile.

[*Canis* (*Lupulus*)] *magellanicus*: Trouessart, 1897:306 (name combination).

Canis montanus Prichard, 1902:260; type locality "South-eastern Patagonia." Preoccupied by *Canis montanus* Marsh, 1871.

Canis amblyodon Philippi, 1903:158; type locality "provincia Valparaiso," Chile.

Canis albigula Philippi, 1903:159; type locality "provinciis centralibus," Chile.

[*Canis* (*Cerdocyon*)] *magellanicus*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*)] *lycoïdes*: Trouessart, 1904:234 (name combination).

[*Canis* (*Cerdocyon*)] *prichardi* Trouessart, 1904:234 (new name for *Canis montanus* Prichard, 1902).

Canis (*Angusticeps*) *reissii* Hilzheimer, 1906:116; type locality "Quito," Pichincha, Ecuador.

Speothos Riveti Trouessart, 1906:1185; type locality "Alchipichi, province de Pichincha (Equateur), altitude de 2101^{m}."

Canis (*Cerdocyon*) *magellanicus Riveti*: Trouessart, 1910:12 (name combination).

C[*anis*]. *Riveti*: Cabrera, 1912:63 (name combination).

Ps[*eudalopex*]. *c*[*ulpaeus*]. *magellanicus*: Thomas, 1914a:357 (name combination).

Ps[*eudalopex*]. *c*[*ulpaeus*]. *culpaeus*: Thomas, 1914a:357 (name combination).

Ps[*eudalopex*]. *lycoides*: Thomas, 1914a: 357 (name combination).

Ps[*eudalopex*]. *c*[*ulpaeus*] *reissii*: Thomas, 1914a:357 (name combination).

Pseudalopex culpaeus andina Thomas, 1914a:357; type locality "Esperanza, near Mt. Sajama, Province of Oruro [La Paz], Bolivia. Alt. 4000 m."

Pseudalopex culpaeolus Thomas, 1914a: 359; type locality "Santa Elena," Soriano, Uruguay. Considered a composite (skin of *P. culpaeus*; skull of *P. gymnocercus*) by Langguth (1967) who selected the skin as lectotype, thus treating the taxon as an objective synonym of *P. inca* Thomas, 1914a, and a subjective synonym of *P. culpaeus andina* Thomas, 1914a.

Pseudalopex inca Thomas, 1914a:361; type locality "Sumbay, Arequipa, Peru. Alt. 4000 m." Considered a composite (skin of *P. gymnocercus*; skull of *P. culpaeus*) by Langguth (1967) who selected the skull as lectotype, thus treating the taxon

as an objective synonym of *P. culpaeolus* Thomas, 1914a, and a subjective synonym of *P. culpaeus andina* Thomas, 1914a.

Canis culpaeus reissi: Osgood, 1914:172 (name combination).

Pseudalopex smithersi Thomas, 1914b:573; type locality "Sierra de Cordoba," Cordoba, Argentina; restricted by Cabrera (1958:232) to Pampa de Achala, 2200 m.

Canis culpaeus andinus: Osgood, 1916:211 (name combination).

Pseudalopex magellanicus: Lönnberg, 1919:1 (name combination).

Pseudalopex culpaea Thomas, 1921:385 (unjustified emendation of gender termination for *culpaeus*).

Pseudalopex reissii: Lönnberg, 1921:23 (name combination).

Canis ferrugineus Huber, 1925:9; type locality "la Cordillera [de los Andes], entre low ríos Mendoza, Atuel, Neuquén y Collun-Curá," Argentina.

[*Canis* (] *Pseudalopex*[)] *gymnocercus culpaeola*: Kraglievich, 1930:52; (name combination).

[*Canis* (] *Dusicyon*[)] *lycoides*: Kraglievich, 1930:58; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus magellanicus*: Kraglievich, 1930:58; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus andinus*: Kraglievich, 1930:59; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus reissii*: Kraglievich, 1930:59; (name combination).

[*Canis* (] *Dusicyon*[)] *culpaeus Riveti*: Kraglievich, 1930:60; (name combination).

[*Canis* (] *D*[*usicyon*)]. *smithersi*: Kraglievich, 1930:60; (name combination).

[*Canis* (] *Dusicyon*[)] *inca*: Kraglievich, 1930:61; (name combination).

Pseudalopex culpaeus andina: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus reissii: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus smithersi: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus magellanica: Cabrera, 1931:63 (name combination).

Pseudalopex culpaeus lycoides: Cabrera, 1931:63 (name combination).

Dusicyon (*Dusicyon*) *culpaeus*: Osgood, 1934:49 (name combination).

Canis magellanicus priscus Spillmann, 1938:387 (*nomen nudum*).

Dusicyon culpaeus andinus: Osgood, 1943: 64 (name combination).

Dusicyon culpaeus lycoides: Osgood, 1943: 66 (name combination).

Dusicyon culpaeus magellanicus: Osgood, 1943:65 (name combination).

Dusicyon [(*Dusicyon*)] *culpaeolus*: Cabrera, 1958:229 (name combination).

Dusicyon [(*Dusicyon*)] *culpaeus reissii*: Cabrera, 1958:232 (name combination).

Dusicyon [(*Dusicyon*)] *culpaeus smithersi*: Cabrera, 1958:232 (name combination).

Dusicyon [(*Dusicyon*)] *inca*: Cabrera, 1958: 235 (name combination).

Comments.—*Lycalopex culpaeus* occurs from the Andes of Colombia to Tierra del Fuego, is widely distributed in Patagonia, but is not known from Paraguay, Uruguay, or Brazil. The species has not been revised since Cabrera's (1958) catalog in which he recognized five subspecies in addition to the nominate form. Langguth (1967) presented convincing arguments that *Pseudalopex culpaeolus* and *P. inca,* both described by Thomas (1914a), were based on composites. Langguth reduced both names to the synonymy of *Pseudalopex* (= *Lycalopex*) *culpaeus.*

Lycalopex gymnocercus (Fischer, 1814)

Synonyms.—

Canis lagopus Molina, 1782:272; type locality "Arcipelago di Chiloe," Chiloé, Chile. Preoccupied by *Canis lagopus* Linnaeus, 1758.

Procyon gymnocercus Fischer, 1814:178; based solely on "L'Agourachay" of Aza-

ra (1801:317); therefore, type locality is Paraguay; restricted by Cabrera (1958: 235) to vicinity of Asunción.

Can[*is*]. *brasiliensis* Schinz, 1821:220; type locality "Brasilien und Paraguay." Based solely on "L'Agourachay of Azara (1801: 317); therefore, restricted type locality is vicinity of Asunción, Paraguay (Cabrera 1958:235).

Canis Azarae s. *Brasiliensis*: Rengger, 1830:143 (name combination).

C[*anis*]. *griseus* Gray, 1837a:88 (*nomen nudum*).

Vulpes fulvipes Martin, 1837:11; type locality "island of Chiloe," restricted by Darwin (*in* Waterhouse 1839) to "sea-beach at the southern point of the island," near San Pedro channel, Chiloé, Chile.

Vúlpes gríseus Gray, 1837b:578; type locality "Magellan," Magellanes, Chile.

Cerdocyon fulvipes: Hamilton-Smith, 1839: 257 (name combination).

C[*anis*]. *protalopex* Lund, 1839a:223 (*nomen nudum*).

Canis protalopex Lund, 1839b:32 (*nomen nudum*).

Canis protalopex Lund, 1840:54, text to plate 28 (fig. 9); type locality "Rio das Velhas," Lagoa Santa, Minas Gerais, Brazil.

Canis [(*Pseudalopex*)] *gracilis* Burmeister, 1861:406; type locality "die buschige Pampa in den Umgebungen Mendozas," Mendoza, Argentina.

Canis patagonicus Philippi, 1866:116; type locality "Magellans Strasse," Magellanes, Chile.

Pseudalopex griseus: Gray, 1869:512 (name combination).

Thous fulvipes: Gray, 1869:514 (name combination).

Canis azarae fossilis Gervais and Ameghino, 1880:36 (*nomen nudum*).

Canis Azarae m. *fossilis* Ameghino, 1889: 298; type locality "Rio Lujan y Cañada de Rocha en los partidos de Mercedes y Lujan, provincia de Buenos Aires," Argentina. Preoccupied by *Canis familiaris fossilis* Pictet, 1853.

Canis Azarae, m. *antiguus* Ameghino, 1889:298; type locality "Rio Lujan en los partidos de Mercedes y Lujan, provincia de Buenos Aires," Argentina.

Canis azarae (var. *fulvipes*): Mivart, 1890a: fig. 25 (name combination).

[*Canis* (*Thous*)] *griseus*: Trouessart, 1897: 307 (name combination).

[*Canis* (*Thous*)] *gracilis*: Trouessart, 1897: 308 (name combination).

Canis domeykoanus Philippi, 1901:168 (p. 4 in reprint); type locality "Provincia de Copiapó," Chile.

Canis rufipes Philippi, 1901:168 (p. 4 in reprint); type locality not given, assumed to be Chile. Most likely a *lapsus* for *Canis fulvipes* (Martin, 1837).

Canis maullinicus Philippi, 1903:158; type locality "provincia Llanquihue ad occidentem lacus Llanquihue, loco 'Nueva Braunau," Chile.

Canis trichodactylus Philippi, 1903:158; type locality "provincia Valdivia," Chile.

Canis torquatus Philippi, 1903:159; type locality "Puerto Montt," Llanquihue, Chile.

[*Canis* (*Cerdocyon*) *azarae*] *protalopex*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*) *azarae*] *antiguus*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*) *azarae*] *fulvipes*: Trouessart, 1904:233 (name combination).

[*Canis* (*Cerdocyon*)] *griseus*: Trouessart, 1904:234 (name combination).

[*Canis* (*Cerdocyon*) *griseus*] *gracilis*: Trouessart, 1904:234 (name combination).

[*Canis* (*Cerdocyon*)] *domeykoanus*: Trouessart, 1904:234 (name combination).

Cerdocyon griseus: J. A. Allen, 1905:155 (name combination).

Pseudalopex azarica Thomas, 1914a:360; type locality "Mar del Plata, S. E. Buenos Ayres," Argentina.

Canis (*Pseudalopex*) *gymnocercus*: Osgood, 1915:143 (name combination).
Pseudalopex domeykoanus: Cabrera, 1917: 27 (name combination).
Canis Domeycoanus: Wolffsohn, 1918:61 (incorrect subsequent spelling of *domeykoanus* Philippi).
Pseudalopex zorrula Thomas, 1921:383; type locality "Chumbicha, Catamarca[, Argentina]. Alt. 500 m."
P[*seudalopex*]. *domeycoanus*: Wolffsohn, 1921:514 (incorrect subsequent spelling of *domeykoanus* Philippi).
C[*anis*]. *cinereo argenteus*: Larrañaga, 1923:344 (not *Canis cinereo argenteus* Schreber, 1775).
C[*erdocyon*]. *t*[*hous*]. *brasiliensis*: G. M. Allen, 1923:56 (name combination).
[*Canis* (] *Pseudalopex*[)] *patagonicus gracilis*: Kraglievich, 1930:50 (name combination; however, *gracilis* has priority over *patagonicus*).
[*Canis* (] *Pseudalopex*[)] *patagonicus zorrula*: Kraglievich, 1930:51 (name combination).
[*Canis* (] *Pseudalopex*[)] *gymnocercus attenuatus* Kraglievich, 1930:54; type locality "los Estados brasileños de Río Grande del Sur, Paraná y tal vez Matto Grosso."
Pseudalopex gymnocercus gymnocercus: Cabrera, 1931:64 (name combination).
Pseudalopex gymnocercus antiguus: Cabrera, 1931:64 (name combination).
Pseudalopex gracilis zorrula: Cabrera, 1931:65 (name combination).
Pseudalopex gracilis domeykoanus: Cabrera, 1931:65 (name combination).
Pseudalopex gracilis patagonicus: Cabrera, 1931:65 (name combination).
Pseudalopex fulvipes: Cabrera, 1931:66 (name combination).
Dusicyon (*Dusicyon*) *gymnocercus*: Osgood, 1934:49 (name combination).
Dusicyon (*Dusicyon*) *griseus*: Osgood, 1934:49 (name combination).
Dusicyon griseus domeykoanus: Osgood, 1943:69 (name combination).
Dusicyon griseus maullinicus: Osgood, 1943:70 (name combination).
Dusicyon fulvipes: Osgood, 1943:71 (name combination).
Ducicyon griseus domeicoanus Mann, 1950:5 (incorrect subsequent spellings of *Dusicyon* Hamilton-Smith, 1839 and *domeykoanus* Philippi, 1901).
Dusicyon [(*Dusicyon*)] *griseus gracilis*: Cabrera, 1958:233 (name combination).
Dusicyon [(*Dusicyon*)] *gymnocercus antiguus*: Cabrera, 1958:234 (name combination).

Comments.—*Lycalopex gymnocercus* occurs from southern Bolivia and Brazil to Tierra del Fuego. Previously considered to represent two species, *gymnocercus* was the name used for the northern and northeastern populations; *griseus,* for the western and southern populations. Kraglievich (1930: 49) used the name *Canis* (*Pseudalopex*) *patagonicus* Philippi, 1866, for the taxon currently known in the literature as *Pseudalopex griseus* (Gray) because he, along with Cabrera (1931), believed *Canis griseus* Gray (1837a) to be preoccupied by *Canis griseus* Boddaert, 1784. However, Gray's name is a *nomen nudum*; the correct original name combination is *Vulpes griseus* Gray (1837b) a junior synonym of *Lycalopex gymnocercus.* Instead of *patagonicus,* Cabrera (1931:65) used *Pseudalopex gracilis* Burmeister, 1861, as the earliest available name for the taxon he later (1958:233) called *Dusicyon griseus* (= *Lycalopex gymnocercus*). Because we have not attempted a complete revision of *L. gymnocercus,* we are reluctant to identify any populations as representing subspecies. Nevertheless, the name *griseus* Gray is available for the southernmost Argentine and Chilean population and *fulvipes* Martin is the appropriate name for the Chiloé Island and adjacent mainland population, which until recently had been considered a separate species.

Canis azarae fossilis has been attributed to Gervais and Ameghino (1880:36); however, the taxon was not described in that

publication, hence it is a nomen nudum because the references to Bravard are not valid indications, since Bravard's work was never actually published (Simpson 1940). The name dates from Ameghino (1889) and is preoccupied. Wozencraft (1993:284) included [*Canis*] *entrerianus* Burmeister, 1861, under *Pseudalopex gymnocercus,* but the type is a male *Cerdocyon thous* (see Thomas 1914a:359, footnote; Cabrera 1931:61; Berta 1982).

Lycalopex sechurae (Thomas, 1900)

Synonyms.—

Canis sechurae Thomas, 1900:148; type locality "Sullana," Piura, Perú.

[*Canis* (*Cerdocyon*)] *sechurae*: Trouessart, 1904:234 (name combination).

Pseudalopex sechurae: J. A. Allen, 1916: 122 (name combination).

[*Canis* (] *Pseudalopex*[)] *sechurae*: Kraglievich, 1930:51 (name combination).

Dusicyon (*Dusicyon*) *sechurae*: Osgood, 1934:49 (name combination).

Comments.—Lycalopex sechurae is monotypic and restricted in distribution to the coastal desert and arid inter-Andean valleys of northwestern Perú and southern Ecuador. Its southern limits in western Perú are not known. Osgood (1914) recorded it in Depto. La Libertad, and it may occur farther south along the Pacific coast.

Lycalopex vetulus (Lund, 1842)

Synonyms.—

Canis azarae: Lund, 1837:324 (not *Canis azarae* Wied, 1824).

Canis vetulus Lund, 1842a:5; type locality "*Rio das Velhas's* Floddal," Lagoa Santa, Minas Gerais, Brazil.

Canis fulvicaudus Lund, 1843:20; type locality "Rio das Velhas's Floddal," Lagoa Santa, Minas Gerais, Brazil.

Vulpes vetulus: Gerrard, 1862:88 (name combination).

[*Lycalopex fulvicaudus*] var. 1. *chilensis* Gray, 1869:511; type locality "Chiloe," Chile. According to Thomas (1904:236), the type locality is wrong.

Canis parvidens Mivart, 1890a:76; type locality "Brazil."

Canis urostictus Mivart, 1890a:81; type locality "Brazil."

[*Canis* (*Thous*)] *parvidens*: Trouessart, 1897:308 (name combination).

[*Canis* (*Thous*)] *urostictus*: Trouessart, 1897:308 (name combination).

Nothocyon urostictus: Wortman and Matthew, 1899:125 (name combination).

Nothocyon parvidens: Wortman and Matthew, 1899:126 (name combination).

Canis sladeni Thomas, 1904:235; type locality "Santa Anna de Chapada," Matto Grosso, Brazil.

[*Canis* (*Nothocyon*)] *parvidens*: Trouessart, 1904:235 (name combination).

[*Canis* (*Nothocyon*)] *urostictus*: Trouessart, 1904:235 (name combination).

E[*unothocyon*]. *sladeni*: J. A. Allen, 1905: 152, footnote (name combination).

E[*unothocyon*]. *urostictus*: J. A. Allen, 1905:152, footnote (name combination).

E[*unothocyon*]. *parvidens*: J. A. Allen, 1905:152, footnote (name combination).

Canis (*Eunothocyon*) *vetulus*: Ihering, 1911:206 (name combination).

Canis Vitulus Huber, 1925:1 (incorrect subsequent spelling of *Canis vetulus* Lund, 1842a).

Lycalopex vetulus: Kraglievich, 1930:43 (name combination).

[*Lycalopex*] *vetulus fulvicaudus*: Kraglievich, 1930:43 (name combination).

Dusicyon (*Lycalopex*) *vetulus*: Osgood, 1934:49 (name combination).

P[*seudalopex*]. *vetulus*: Berta, 1987:458 (name combination).

Comments.—Lycalopex vetulus is monotypic and found only in Brazil, although Berta (1987) mentioned a fossil from Argentina. Mivart's names *Canis parvidens* and *C. urostictus* have been cited from his report in the Proceedings of the Zoological Society of London (1890b); however, that

paper was published in August 1890 (Duncan 1937) after his monograph on the Canidae, which was listed in volume 12(8) of Nature Novitates for May 1890.

Literature Cited

Allen, G. M. 1923. The pampa fox of the Bogota savanna.—Proceedings of the Biological Society of Washington 36:55–58.

Allen, J. A. 1905. Mammalia of southern Patagonia. *In* W. B. Scott, ed., Reports of the Princeton University Expeditions to Patagonia, 1896–1899, 3(part 1):1–210, 29 pls.

———. 1916. List of mammals collected for the American Museum in Ecuador by William B. Richardson, 1912–1913.—Bulletin of the American Museum of Natural History 35:113–125.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la Republica Argentina.—Acta Academia Nacional de Ciencias de la Republica Argentina en Córdoba, Buenos Aires 6:xxxii + 1–1027 pp.; atlas, 98 pls.

Azara, F. 1801. Essais sur l'histoire naturelle des quadrupedes de la province du Paraguay. Traduits sur le manuscrit inédit de l'auteur, Pra. M. L. E. Moreau-Saint-Méry. Charles Pougens, Paris, 1:lxxx + 366 pp.

Berta, A. 1982. Cerdocyon thous.—Mammalian Species 186:1–4.

———. 1987. Origin, diversification, and zoogeography of the South American Canidae. Pp. 455–471 *in* B. D. Patterson and R. M. Timm, eds., Studies in neotropical mammalogy. Essays in honor of Philip Hershkovitz.—Fieldiana, Zoology 39:vii + 1–506.

———. 1988. Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora).—University of California Publications, Geological Sciences 132:x + 1–149, 10 pls.

Burmeister, H. 1854. Systematische Uebersicht der Thiere Brasiliens, welche während einer Reise durch die Provinzen von Rio de Janeiro und Minas Geraës gesammelt oder beobachtet wurden von Dr. Hermann Burmeister. Säugethiere (Mammalia). Georg Reimer, Berlin, 1:x + 342 pp.

———. 1856. Erläuterungen zur Fauna Brasiliens, enthaltend Abbildungen und ausführliche Beschreibungen neuer oder ungenügend bekannter Thier-Arten. Georg Reimer, Berlin, ix + 115 pp., 32 pls.

———. 1861. Reise durch die La Plata-Staaten, mit besonderer Rücksicht auf die Beschaffenheit und den Culturzustand der Argentinischen Republik Ausgführt in den Jahren 1857, 1858, 1859 und 1860. H. W. Schmidt, Halle, 2:vi + 538 pp., 1 map.

Cabrera, A. 1912. Catálogo Metódico de las Colecciones de Mamíferos del Museo de Ciencias Naturales de Madrid.—Trabajos del Museo de Ciencias Naturales, Número 11:1–147, 4 pls.

———. 1917. Mamíferos del viaje al Pacífico verificado de 1862-1865 por una comisión de naturalistas enviada por el gobierno Español.—Trabajos del Museo Nacional de Ciencias Naturales, Serie Zoológica, Número 31:1–62.

———. 1931. On some South American canine genera.—Journal of Mammalogy 12:54–67.

———. 1932. Sinopsis de los cánidos argentinos.—Revista del Centro de Ingenieros Agrónomos y Centro de Estudios de Agronomía 145:489–501.

———. 1940. Notas sobre carnívoros sudamericanos.—Instituto del Museo de la Universidad Nacional de La Plata 5(29):1–22.

———. 1958. Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Zoologia 4(1):1–308. [Dated 1957; published 27 March 1958—see notice on p. 308.]

———, & J. Yepes. 1940. Mamíferos Sud-americanos. Compañía Argentina de Editores, Buenos Aires, 370 pp.

Chehébar, C., & S. Martín. 1989. Guía para el reconocimiento de los pelos de los mamíferos de la Patagonia.—Doñana, Acta Vertebrata 16(2): 247–291.

Clutton-Brock, J., G. B. Corbet, & M. Hills. 1976. A review of the family Canidae, with a classification by numerical methods.—Bulletin of the British Museum (Natural History), Zoology 29(3):119–199.

Corbet, C. B., & J. E. Hill. 1991. A World list of mammalian species. Third edition. Natural History Museum Publications, London, and Oxford University Press, New York, viii + 243 pp.

Duncan, F. M. 1937. On the dates of publication of the Society's 'Proceeding,' 1859–1926. With an Appendix containing the dates of Publication of 'Proceedings,' 1839–1858, compiled by the late F. H. Waterhouse, and of the 'Transactions,' 1833–1869, by the late Henry Peavot, originally published in P.Z.S. 1893, 1913.—Proceedings of the Zoological Society of London 107(A): 71–84.

Fischer, G. 1814. Zoognosia tabulis synopticis illustrata. Volumen tertium. Quadrupedum reliquorum, cetorum et montrymatum descriptionem continens. Nicolai Sergeidis Vsevolozsky, Mosquae, 3:xxiv + 1–732.

Fuentes, E. R., & F. M. Jaksic. 1979. Latitudinal size variation of chilean foxes: tests of alternative hypotheses.—Ecology 60(1):43–47.

Gallardo, M., & J. R. Formas. 1975. The karyotype of *Dusicyon griseus* (Carnivora, Canidae).—Experientia 31(6):639–640.

Gerrard, E. 1862. Catalogue of the bones of Mammalia in the collection of the British Museum. British Museum (Natural History), London, iv + 296 pp.

Gervais, H., & F. Ameghino. 1880. Les mammifères fossiles de l'Amérique du Sud. F. Savy, Paris, xii + 225 pp.

Gingerich, P. D., & D. A. Winkler. 1979. Patterns of variation and correlation in the dentition of the red fox, *Vulpes vulpes*.—Journal of Mammalogy 60(4):691–704.

Gray, J. E. 1837a. [Characters of some new species of *Mammalia* in the Society's Collection, with remarks upon the dentition of the *Carnivora,* and upon the value of the characters used by M. Cuvier to separate the *plantigrade* from the *digitigrade Carnivora.*]—Proceedings of the Zoological Society of London 1836:87–88.

———. 1837b. Description of some new or little known Mammalia, principally in the British Museum Collection.—The Magazine of Natural History, and Journal of Zoology, Botany, Mineralogy, Geology, and Meteorology 1:577–587.

———. 1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum (Natural History), London, xxviii + 216 pp.

———. 1869. Notes on the skulls of the species of dogs, wolves, and foxes (*Canidae*) in the collection of the British Museum.—Proceedings of the Zoological Society of London 1868:492–525.

Hamilton-Smith, C. 1839. The natural history of dogs. Vol. I. The Naturalists Library, W. Jardine, ed. W. H. Lizars, Edinburgh, 9:frontispiece, i–xiv, 15–267, 33 pls.

Hilzheimer, M. 1906. Papio mundamensis, Felis deliensis, Canis reissii und andre neue Säugethiere.—Zoologischer Anzeiger 30:109–118.

Huber, A. 1925. El zorro y su piel in la República Argentina.—Republica Argentina, Ministerio de Agricultura, Sección Propaganda e Informes, Numero 360, 11 pp.

Ihering, H. von. 1911. Os mammíferos do Brazil Meriodinal.—Revista do Museo Paulista, São Paulo 8:147–275.

Kerr, R. 1792. The animal kingdom or zoological system, of the celebrated Sir Charles Linnaeus. Class I. Mammalia: containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the mammalia, or animals which give suck to their young; being a translation of that part of the systema naturae, as lately published, with great improvements, by Professor Gmelin of Goettingen. Together with numerous additions from more recent zoological writers, and illustrated with copperplates. A. Strahan, T. Cadell, and W. Creech, Edinburgh, xii, 1–32 + 32 (unnumbered) + 33–400, 7 pls.

Kraglievich, L. 1930. Craneometria y clasificación de los cánidos sudamericanos, especialmente los argentinos, actuales y fósiles.—Physis 10:35–73, 7 pls.

Langguth, A. 1967. Sobre la identidad de *Dusicyon culpaeolus* (Thomas) y de *Dusicyon inca* (Thomas).—Neotropica 13:21–28.

———. 1969. Die südamerikanischen Canidae unter besonderer berücksichtigung des mähnenwolfes *Chrysocyon brachyurus* Illiger.—Zeitschrift für Wissenschaftliche Zoologie 179(1–2):1–188.

———. 1975. Ecology and evolution in the South American canids. Pp. 192–206 *in* M. W. Fox, ed., The wild canids, their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Co, New York, xviii + 508 pp.

Larrañaga, D. A. 1923. Escritos. Instituto Histórico y Geográfico del Uruguay, Montevideo, 2:1–512 + 2 tables.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentii Salvii, Holmiae, 1:1–824.

Lönnberg, E. 1919. Remarks on some South American Canidae.—Arkiv för Zoologi, Stockholm 12(13):1–18.

———. 1921. A second contribution to the mammalogy of Ecuador with some remarks on *Caenolestes*.—Arkiv för Zoologi, Stockholm 14(4):1–104.

Lund, P. W. 1837. Om Huler i Kalksteen i det indre af Brasilien der tildeels indeholde fossile Knokler. Anden Afhandling. Lappa da Cerca Grande.—Kongelige Danske, Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 6:307–332, pls. 1–3.

———. 1839a. Coup-d'oeil sur les espèces éteintes de Mammifères du Brésil, extrait de quelques mémoires présentés à l'Académie royale des Sciences de Copenhague.—Annales des Sciences Naturelles, Seconde Série 11:214–234.

———. 1839b. Pattedyrene.—Kongelige Danske, Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger, 82 pp., 13 pls. [Repaged preprint of Lund 1841a.]

———. 1840. Fortsaettelse af Pattedyrene.—Kongelige Danske, Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger, 56 pp., 11 pls. [Re-paged preprint of Lund 1841b.]

———. 1841a. Blik paa Brasiliens Dyreverden för sidste Jordomvaeltning. Anden Afhandling: Pat-

tedyrene.—Kongelige Danske, Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 8:63–144, pls. 1–13.

———. 1841b. Blik paa Brasiliens Dyreverden för sidste Jordomvaeltning. Tredie Afhandling: Fortsaettelse af Pattedyrene.—Kongelige Danske, Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 8:219–272.

———. 1842a. Fortsatte Bemaerkninger over Brasiliens uddöde Dyrskagning.—Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 3:1–16. [Repaged preprint of Lund 1842b.]

———. 1842b. Fortsatte Bemaerkninger over Brasiliens uddöde Dyrskagning.—Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 9:121–136.

———. 1843. Fortsaettelse af Pattedyrene. Om de nulevende og uddöde Arter af Rovdyrenes Familie paa det tropiske Brasiliens indre höisletter. Förste Afdeling: Hundegruppen.—Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 5:1–82, 7 pls. [Re-paged preprint of Lund 1845.]

———. 1845. Blik paa Brasiliens Dyreverden för sidste Jordomvaeltning. Femte Afhandling. Fortsaettelse af Pattedyrene. Om de nulevende og uddöde Arter af Rovdyrenes Familie.—Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 11:1–82, pls. 40–46.

Mann F., G. 1950. Nuevos mamíferos de Tarapacá.—Investigaciones Zoológicas Chilenas 2:4–6.

Martin, W. 1837. [Observations upon a new fox from Mr. Darwin's Collection (*Vulpes fulvipes*).]—Proceedings of the Zoological Society of London 1837:11–12.

Mivart, St. G. 1890a. Dogs, jackals, wolves, and foxes: a monograph of the Canidae. R. H. Porter, London, xxxvi + 216 pp., 45 pls. [Published by April, 1890; see Nature Novitates, Berlin 12(8): 171.]

———. 1890b. Notes on the South-American *Canidae*.—Proceedings of the Zoological Society of London 1890:98–113. [Published August, 1890; see Duncan 1937.]

Molina, G. I. 1782. Saggio sulla storia naturale del Chili. Stamperia di S. Tommaso d'Aquino, Bologna, 367 pp., 1 map.

Nowak, R. M. 1991. Walker's mammals of the World. Fifth edition. The John Hopkins University Press, London, 2:x + 643–1629.

Osgood, W. H. 1914. Mammals of an expedition across northern Peru.—Field Museum of Natural History, Zoölogical Series 10:143–185.

———. 1915. The name of Azara's agouarachay.—Proceedings of the Biological Society of Washington 28:142–143.

———. 1916. Mammals of the Collins-Day South American Expedition.—Field Museum of Natural History, Zoölogical Series 10:199–216, plates 6–7.

———. 1934. The genera and subgenera of South American canids.—Journal of Mammalogy 15: 45–50.

———. 1943. The mammals of Chile.—Field Museum of Natural History, Zoological Series 30: 1–268.

Philippi, R. A. 1866. Ueber ein paar neue Chilenische Säugethiere.—Archiv für Naturgeschichte 32(1):113–117.

———. 1896. Dos animales nuevos de la fauna Chilena.—Anales de la Universidad de Santiago de Chile 94:541–546. [Reprint pages 1–6.]

———. 1901. Nueva especie Chilena de zorras.—Anales de la Universidad de Santiago de Chile 108:167–170, 1 pl.

———. 1903. Einige neue Chilenische Canis-Arten.—Archiv für Naturgeschichte 69(1):155–160.

Prichard, H. H. 1902. Through the heart of Patagonia. D. Appleton and Company, New York, xvi + 346 pp., 40 pls.

Rengger, J. R. 1830. Naturgeschichte der Saeugethiere von Paraguay. Schweghauserschen, Basel, xvi + 394 pp.

Rohlf, F. J. 1992. NTSYS-PC: numerical taxonomy and multivariate analysis system. Version 1.70. Ser. 1459CV. Exeter Software.

Schinz, H. R. 1821. Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschichte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier. Erster band. Säugethiere und Vögel. J. G. Cotta'schen Buchhandlung, Stuttgart und Tübingen, 1:xxxviii + 894 pp.

Simpson, G. G. 1940. The names *Mesotherium* and *Typotherium*.—American Journal of Science 238:518–521.

———. 1945. The principles of classification and a classification of mammals.—Bulletin of the American Museum of Natural History 85:xvi + 1–350.

Spillmann, F. 1938. Die fossilen Pferde Ekuadors der Gattung *Neohippus*.—Palaeobiologica 6:372–393.

Thomas, O. 1900. New South-American mammals.—Annals and Magazine of Natural History, Series 7, 5:148–153.

———. 1904. On the mammals collected by Mr. A. Robert at Chapada, Matto Grosso (Percy Sladen Expedition to Central Brazil).—Proceedings of the Zoological Society of London 1903, 2(2): 232–244, plate 27.

———. 1914a. On various South-American mammals.—Annals and Magazine of Natural History, Series 8, 13:345–363.

———. 1914b. Three new S.-American mammals.—Annals and Magazine of Natural History, Series 8, 13:573–575.

———. 1921. New foxes of the genera *Cerdocyon* and *Pseudalopex* from northern Argentina.—Annals and Magazine of Natural History, Series 9, 7:381–385.

Trouessart, E.-L. 1897. Catalogus mammalium tam viventium quam fossilium. Fasciculus II. Carnivora, Pinnipedia, Rodentia I. R. Friedländer and Sohn, Berolini, 1:219–452.

———. 1904. Catalogus mammalium tam viventium quam fossilium. Quinquennale supplementium, anno 1904, Fascicule 1, pp. 1–288. R. Friedländer and Sohn, Berolini, vii + 929 pp.

———. 1906. Sur une espèce nouvelle du genre Icticyon (*Speothos*), provenant de l'Equateur.—Comptes Rendus des Séances de l'Académie des Sciences 143:1184–1186.

———. 1910. Mammifères de la Mission de l'Équateur d'apres les collections formées par le Dr. Rivet. Pp. 1–32, 8 plates *in* Mission du Service Géographique de l'Armée pour la mesure d'un arc de méridien équatoriale en Amérique du Sud sus le Controle Scientifique de l'Académie de Sciences, 1899-1906. Tome 9, Zoologie. Fascicule 1.—Mammifères, Oisseux, Trochilidae. Ministère del'Instruction Publique, Paris. [Dated 1911; published November 24, 1910.]

Van Gelder, R. G. 1978. A review of canid classification.—American Museum Novitates 2646:1–10.

Vitullo, A. D., & G. A. Zuleta. 1992. Cytogenetics and fossil record: confluent evidence for speciation without chromosomal change in South American canids.—Zeitschrift für Säugetierkunde 57:248–250.

Waithman, J., & A. Roest. 1977. A taxonomic study of the kit fox, *Vulpes macrotis*.—Journal of Mammalogy 58:157–164.

Waterhouse, G. R. 1839. Mammalia. Pp. 49–97 *in* C. Darwin, ed., The zoology of the voyage of the H.M.S. Beagle under the command of Captain Fitzroy, R. N., during the years 1832–1836. Smith, Elder and Company, London, 2:xii + 97 pp., 35 pls., 1838–1839.

Wolffsohn, J. A. 1918. Reseña de los trabajos publicados desde 1895 por autores nacionales y extranjeros sobre la mamalogia chilena.—Actes de la Société Scientifique du Chili 23:57–79.

———. 1921. Catalogo de craneos de mamíferos de Chile colectados entre los años 1896–1918.—Revista Chilena de Historia Natural 25:511–529.

Wortman, J. L., & W. D. Matthew. 1899. The ancestry of certain members of the Canidae, the Viverridae, and Procyonidae.—Bulletin of the American Museum of Natural History 12:109–138, 1 table, 1 pl.

Wozencraft, W. C. 1989. Classification of the Recent Carnivora. Pp. 569–593 *in* J. L. Gittleman, ed., Carnivore behavior, ecology and evolution. Cornell University Press, Ithaca, New York, xvi + 620 pp.

———. 1993. Order Carnivora. Pp. 279–348 *in* D. E. Wilson and D. M. Reeder, eds., Mammal species of the World: a taxonomic and geographic reference, Second Edition. Smithsonian Institution Press, Washington, D.C., xvii + 1206 pp.

Appendix 1

List of specimens included in the statistical analyses of craniometry and pelage. OTU acronyms for cranial analyses start with the letter C; those for pelage character analysis start with a "P." Museum acronyms: Museo Argentino de Ciencias Naturales, MACN; Instituto Miguel Lillo, Tucumán, IML.

Craniometric Analysis

Lycalopex culpaeus (*culpeo fox*).—CCU (n = 58). (MACN) JUJUY, Abra Blanca (2): 38.039, 4.041; Lizoite (1): 41.055. NEUQUEN, Catán-Lil (53): 15138–15142, 15147, 15151–15154, 15167, 15169, 15171, 15173–15177, 15181, 15183–15184, 15188, 15190–15192, 15194–15196, 15204, 15207–15208, 15211, 15220, 15221, 15223–15227, 15231, 15235–15236, 15238–15240, 15243–15244, 15247–15248, 15250–15253. SANTA CRUZ, San Julián (2): 19221–19222.

Lycalopex gymnocercus (*gray fox*).—CST (7). (MACN) CHUBUT, Lago Blanco (1): 224; Río Mayo (2): 20207–20208. (MACN) SANTA CRUZ, Río Robles (2): 15692, 16321; (IML) SANTA CRUZ (2): 421–422.

CWT (14). (MACN) MENDOZA, La Paz (1): 1737. (MACN) NEUQUEN, Zapala (1): 14902. (MACN) RIO NEGRO, Pilcaniyeu (4): 20205–20206, 20276, 20278; General Roca (8): 24.050, 24.052–24.054, 24.066, 24.079–24.081.

CNW (8). (MACN) CATAMARCA, Andalgalá (3): 50.419–50.420, 50.432; Salar de Pipanaco (1): 51.170; Singuil (1): 53.002; (IML) CATAMARCA, Belén (1): 895. (MACN) SAN JUAN, Ischigualasto (1): 13781. (IML) SAN JUAN, Valle Fértil (1): 1178.

CCT (33). (MACN) LA PAMPA, Caleu-Caleu (15): 13327, 13331, 13337, 15748–15752, 15754, 49.139, 49.148–49.149, 49.159–49.160, 49.167; Carro Quemado (11): 16120, 16127, 16130, 16136, 16140–16141, 16145, 16147–16150; General Acha (7): 50.489, 50.492–50.493, 50.495–50.496, 50.499, 50.502.

CET (15). (MACN) BUENOS AIRES, (1): 285; Puerto Quequén (1): 14409; Bolívar (2): 15363–15364; Coronel Suárez (4): 15387–15390; Balcarce

(4): 24.133, 24.143, 24.148, 24.156; Azul (1): 26.028; Punta Médano (1): 26.163; Juárez (1): 54.133.

CNT (16). (MACN) CORDOBA, La Paz (1): 29.035; Pampa de Olaén (1): 39.191; Soto (1): 39.194. (MACN) JUJUY, (1): 32.252. (MACN) SALTA, Metán (1): 14323; Dragones (1): 36.480. (MACN) SANTIAGO DEL ESTERO, Cerro Quemado (2): 30.210–30.211; (IML) SANTIAGO DEL ESTERO, La Banda (1): 908; Giménez (1): 959. (MACN) TUCUMAN, Tapia (1); 26.129; Monteros (1): 28.182; (IML) TUCUMAN, Trancas (2): 192, 495; Tafí del Valle (2): 545, 836.

Specimens Analyzed for Pelage Characters

Lycalopex culpaeus (*culpeo fox*).—PCU (27). (MACN) RIO NEGRO, Valcheta (1): 14546; El Manso (1): 16419. (MACN) NEUQUEN, Aluminé (2): 13473, 13475; Catán-Lil (8): 15021–15024, 15030, 16169, 16171, 19223. (MACN) SANTA CRUZ, Puerto San Julián (3): 19221–19222, 50.449. (MACN) CHUBUT, Valle Lago Blanco (1): 207. (MACN) LA RIOJA, Velazco (1): 34.316. (MACN) JUJUY, Cochinoca (1): 39.493; Lizoite (2): 41.055–41.056; Santa Catalina (2): 41.164–41.165. (MACN) TIERRA DEL FUEGO, Río Grande (3): 50.480–50.482. (MACN) SALTA, San Antonio de los Cobres (2): 26.189–26.190.

Lycalopex gymnocercus (*gray fox*).—PET (14). (MACN) BUENOS AIRES, Puerto Quequén (1): 14409; Bolívar (1): 15363; Sierra de La Ventana (9): 36.046–36.050, 36.052–36.055; Rocha (2): 39.713, 39.715; Juárez (1): 54.133.

PNW (6). (MACN) SAN JUAN, Ischigualasto (1): 13781. (MACN) LA RIOJA, Villa Unión (1): 34.562. (MACN) CATAMARCA, Andalgalá (3): 50.419–50.420, 50.432; Singuil (1): 53.002.

PNT (25). (MACN) CORDOBA, (1): 31.195; Bialet Masse (1): 39.190; Soto (1): 39.194; La Paz (1): 29.035; Valle de Los Reartes (1): 25.166; Sobremonte (1): 13299; Sierra de Achala (1): 25.110. (MACN) CHACO, (1): 30.206. (MACN) SALTA, Aguaray (1): 36.228; Metán (2): 14319, 14323; Dragones (2): 36.180, 36.479; Río Caraparí (1): 36.477. (MACN) SANTIAGO DEL ESTERO, Colonia Dora (1): 42.011. (MACN) FORMOSA, Ingeniero Juárez (5): 47.133–47.136, 47.138. (MACN) SAN LUIS, Chacabuco (1): 14707; Chosmes (1): 49.224. (MACN) TUCUMAN, Burruyacú (1): 30.150; Tapia (1): 26.129; Monteros (1): 28.182.

PWT (9). (MACN) MENDOZA, (2): 38.002–38.003; Capital (1): 17827. (MACN) NEUQUEN, Catán-Lil (1): 17828; Junín de Los Andes (1): 38.223. (MACN) CHUBUT, Valle Lago Blanco (4): 209–212.

PCT (30). (MACN) LA PAMPA, Lihuel-Calel (1): 15601; Limay-Mahuida (1): 16357; Caleu-Caleu (14): 49.134–49.136, 49.148, 49.159, 49.167, 49.174–49.181; General Acha (14): 50.483–50.488, 50.492, 50.494, 50.498, 50.501, 50.503–50.505, 50.507.